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INTRODUCTION

Seeing may be convincing evidence of the actuality of a fact, but it does not necessarily impart an understanding of the thing observed. We may, for example, with our own eyes witness the splitting of the skin over the back and head of some young insect, such as the aquatic larva of a dragonfly, and observe the emergence of the winged adult fully equipped for life in the air. The change is so great as to be almost unbelievable if it were not a commonplace event, and yet with all that entomologists now know about insects, this phenomenon of metamorphosis still baffles the understanding.

The young dragonfly (fig. 1) is as perfectly constructed for the life it leads in the water as are its parents for life in the air. The length of the larval life from hatching to maturity may be one, two, three, or even five years, according to the species, and as the larva grows it may shed its outer skin a dozen or more times. At each moult except the last it simply repeats its own structure on a slightly larger scale with a few developmental changes; at the last moult it transforms into a creature entirely different from itself, but which is a replica of one of its parents. Throughout its life, therefore, the dragonfly larva carries some latent power that finally gives rise from the larval tissues to the parental form that produced the egg from which it was hatched.

The structural changes that take place at the transformation of the larva to the adult, according to Whedon (1929), do not appreciably affect the nerve chain, the heart, the Malpighian tubules, or the gonads, all of which develop progressively from embryo to the imago, except that there probably takes place some histological changes in the nerve ganglia, together with an atrophy of larval nerve branches and the formation of new ones in adjustment to the reorganization of the alimentary canal and the muscular system. Metamorphosis, however, brings about great changes in the integument, the musculature of the head and abdomen, the alimentary canal, the fat body, and the tracheal system.

In the dragonfly larva there is none of those special regeneration centers, or "imaginal discs," that in insects of higher orders form the adult tissues from latent embryonic cells while the larval tissues go into dissolution. The special adult structure of the skeleton of the dragonfly, for example, is formed simply by a renewed activity in the larval epidermis during the transformation period that produces an entirely different skeletal structure from that which this same epidermis produced many times before at the larval moults. A change of the same nature takes place in the ectodermal parts of the alimentary canal, though the imaginal mesenteron is regenerated in the usual manner from replacement cells. Muscles of the larval head and abdomen go into dissolution, and are replaced by muscles suitable to the adult, but the thoracic wing muscles simply complete their development, while the wings themselves rapidly take on the adult form and venation.

The metamorphic changes that take place in the dragonflies are undoubtedly, as in other insects, controlled by hormones, though the dragonfly has been neglected as a subject for hormonal study. Corpora cardiaca and allata are both present in the Odonata. The first, according to Cazal (1948), lie on the lateral walls of the aorta behind the brain and are fused with each other above the aorta; they receive the usual four nerves from the brain, and are best developed in large larvae and adults. The corpora allata, Cazal says, are globular or ovoid bodies in young larvae, but in the adult they become elongate and lie in contact with the circumoesophageal nerve connectives. They are innervated through the anterior ends of the corpora cardiaca. In addition to these dorsal incretory organs, small glandular bodies lying ventrally in the posterior part of the head have been described by Pflugfelder (1938, 1947) in Odonata and other insects. They are
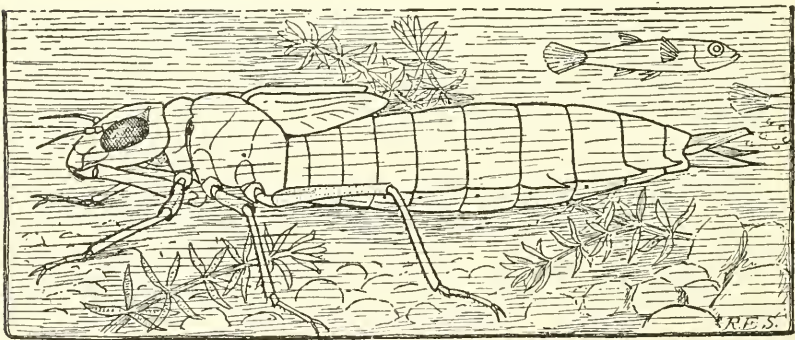

FIG. 1.—*Anax junius* (Drury), larva (x 1¾).

said to be of ectodermal origin and to degenerate after the last moult. From experiments on larvae of *Aeschna cyanea,* Deroux-Stralla (1948) concludes that the ventral glands play an important role in moulting and metamorphosis. She finds that larvae of the penultimate stage from which the glands have been removed moult abnormally or incompletely, while gland removal from last instar larvae results in a complete suppression of metamorphosis. The presence of thoracic endocrine glands has apparently not yet been noted in Odonata. Whedon (1938) suggests that the oenocytes associated with the aortic diverticula, the activity of which is greatly increased in the adult, may have some endocrine function.

Hormones, of course, have nothing to do with the *kind* of structural changes that will take in the tissues at metamorphosis. The course of development may be inhibited or released from inhibition by hormones, but it is determined in advance by the hereditary factors inherent in the tissues, which go into action when the hormonal balance creates the proper environment.

From the work of investigators on insect hormones in general it is evident that the corpus-allatum hormone has the same function in the young of ametabolous or hemimetabolous insects that it has in holometabolous larvae, which is that of arresting development between moults. We might conclude, therefore, that this hormone primarily had no relation to metamorphosis, since it would appear that any animal having a nonexpansible integument during each of its developmental instars must necessarily have some means of inhibiting the growth of juvenile tissues between moults. However, Wigglesworth (1953) finds that an adult of *Rhodnius* given both moulting hormone and juvenile hormone will moult again, but shows a partial reversion to nymphal characters. He concludes, therefore, that the corpus-allatum hormone is not entirely inhibitory, but has a more *positive* action on the juvenile tissues by actively favoring their differentiation, since it does so even in an imaginal instar.

Several writers have remarked that the metamorphosis of the Odonata is essentially holometabolous, though no pupal stage intervenes between the larva and the imago. The dragonfly at least demonstrates that as great a transformation can be accomplished by a direct change of growth at one moult as many of the so-called holometabolous insects accomplish with two moults. According to Munscheid (1933) the transformation in *Aeschna cyanea* occupies as much as 12 days before the adult comes out of the larval cuticle. The transformation period, therefore, is equivalent to the pupal stage of a holometabolous insect, and from this it might be argued that the pupa represents

the last immature instar of hemimetabolous insects. It must be noted, however, that a pupa has essentially the form of the adult, and externally is a preliminary adult stage with the internal organs not yet completed. If the developing imago of the dragonfly within the larval cuticle shed the larval cuticle at the beginning of its metamorphosis instead of at the end, it would come out as an incomplete adult, and would thus be equivalent to a pupa, though it might complete its development without another moult. According to Whedon (1929) the dissolution of the larval abdominal muscles is not completed until several days after ecdysis.

The reason for the great degree of change made by the dragonfly at the moult to the adult is the disparity between the larval structure and the structure of the imago. The larva is specifically adapted in almost every detail of its organization to life in the water; the adult, on the other hand, is equally adapted to the very different life it leads in the air. In other words, through many millions of years the larva and the imago have been evolving along quite different lines each for its own purpose. The laws of heredity have been suspended, giving the young insect freedom to follow its own evolutionary course, so long as it finally reverts to the parental form. The embryo, therefore, develops directly into the larva, and the hormonal condition within the larva does not allow the forces of adult heredity to assert themselves until the larva has performed its part in the life of the species.

Tillyard (1917) has suggested that the larvae of the Carboniferous Protodonata probably lived in mud and rotting vegetation around the shores of some stagnant lake, and here "began that series of adaptive changes which finally led them to adopt a purely aquatic life." We must assume, however, that the young stages of insects with metamorphosis at some early time in their evolution resembled the adults of their species in the same degree that the young of modern insects without metamorphosis, such as a grasshopper or a cockroach, resemble their parents. The adult Protodonata were already perfect dragonflies in their way, and it is therefore highly improbable that at this stage of odonate evolution the young could have had any likeness to the specialized adults. The adult Protodonata themselves must have had a long line of evolution extending back through a million years or so before they reached the status of Carboniferous dragonflies. The larvae, then, began their divergence from the adult line of evolution when the adults were insects of a much more generalized type of structure than that of the Protodonata. In the body of a modern dragonfly larva the only part that in any way resembles the corresponding part of the adult is the thorax; the specialized adult type

of thorax serves equally well for the larva, and therefore has not been essentially modified in the larval evolution.

Nothing is known of the early odonate larvae, but when they took to the water their first concern must have been with developing some means of aquatic respiration. Inasmuch as a few modern zygopterous larvae have lateral gills along the sides of the abdomen, and in this respect resemble the larvae of mayflies, we may reasonably suppose that the primary odonate larvae were first thus equipped for breathing in the water. This assumption is all the more reasonable if we wish to believe that such gills represented more primitive abdominal styli, such as those still preserved in terrestrial Thysanura. Speculation on the origin and evolution of an animal is quite safe where there is complete ignorance of historical facts.

I. THE HEAD

The larval head is clearly adapted in its shape to the use of the labium as a grasping organ. The head is prognathous (fig. 5 C), the mandibles and maxillae being directed horizontally forward beneath the labrum, where they are in a position to receive the food brought back to them by the prehensile labium. In an aeschnid larva particularly, the head is much flattened (fig. 5 C). The postoccipital margin on which the neck is attached is strongly oblique from above downward and forward to the base of the labium, which latter thus becomes suspended below the center of the cranium to give it a longer forward reach when protracted. The large compound eyes project on the sides of the head (fig. 2 A), but they do not meet on the vertex as they will in the adult (D). The antennae have a forward position just behind the clypeus (A). The broad clypeus (*Clp*) gives articulation to the mandibles on its basal angles, and supports the large labrum (Lm). The cranial walls are braced internally by a well-developed tentorium (B, *Tnt*), consisting of a posterior bridge arising from pits (*pt*) in the anterior ends of the postoccipital sulcus (*pos*), and of posteriorly convergent anterior arms arising from slits between the compound eyes and the bases of the mandibles (A, *at*). Short dorsal branches of the anterior arms are attached on the cranial wall by brushes of apparently nonmuscular fibers. The ventral margins of the cranium (B) surround the neck foramen posteriorly, but are widely divergent anteriorly along the sides of the maxillae. The mandibles and the maxillae are articulated on the cranial margin (a,a') ; the labium (fig. 3 A, *Lb*) is suspended from the membranous ventral head wall behind the hypopharynx and has no direct support on the cranium.

At the time when the aeschnid imago is ready for ecdysis, the larval cuticle splits along the middle of the back on the thorax and the first abdominal segment. On the head (fig. 2 C) the cleavage line continues over the vertex to the frontal region, where it forks laterally around the frons and then curves outward through the corneae of the compound eyes. The ecdysial split on the head follows this course in most
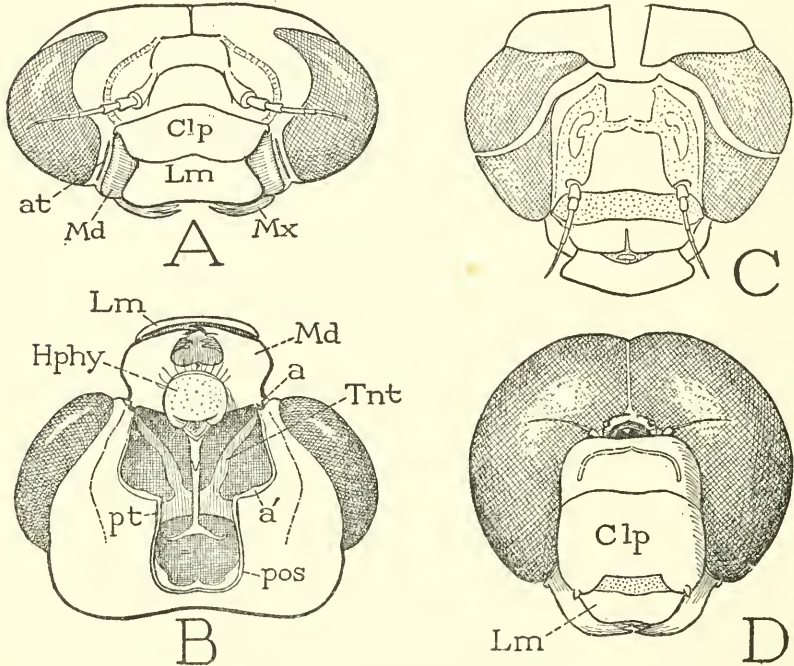

FIG. 2.—*Anax junius* (Drury).

A, head of larva, anterior. B, same, ventral view, with mouth parts and membranous ventral wall of head removed, exposing hypopharyngeal apodeme and tentorium. C, cuticle of larval head after ecdysis, showing open cleavage line. D, head of adult male, anterior.

a, ventral articulation of mandible; *a',* articulation of maxilla; *at,* anterior tentorial pit; *Clp,* clypeus; *hAp,* hypopharyngeal apodeme; *Hphy,* hypopharynx; *Lm,* labrum; *Md,* mandible; *Mx,* maxilla; *pos,* postoccipital sulcus; *pt,* posterior tentorial pit; *Tnt,* tentorium.

Odonata, both at the larval moults and at the final transformation, but it shows variations in different forms and in some it does not invade the eyes.

The head of the adult dragonfly is fully formed within the cuticle of the larval head, but when the emerging insect extracts itself from the larval skin, the head at once takes on a very different shape (fig. 6 G, H). It is now hypognathous, the mouth parts hanging downward.

The occipital foramen has contracted to a small keyhole-shaped open-
ing in the center of the wide, vertical, posterior surface of the cranium,
so that the head is freely movable in all directions on a narrow neck.
In a transforming *Anax* larva the compound eyes of the adult may
be seen within the larval cuticle to have extended mesally behind the
frons. Finally in the imago (fig. 2 D) they all but meet along the
median line, being separated by only a narrow infolding of the head
wall representing the remnant of the larval vertex. The growth of
the eyes during the larval period has been shown by Lew (1934) to
take place by the differentiation of new ommatidia in a "budding-
zone" of the epidermis along the inner margin of each eye, to which
they are added from instar to instar. The greatest increase takes place
at the transformation of the larva to the imago. Three ocelli are
present on the adult head, including a large median ocellus and two
very small lateral ocelli. The antennae have moved upward on the
face until they arise on the upper part of the frons at the sides of the
lateral ocelli. The frontoclypeal region forms a large protruding quad-
rate plaque on the middle of the face closely embraced by the com-
pound eyes.

The head of the adult dragonfly is as clearly adapted in its struc-
ture to the feeding habits of the adult as is the larval head to the feed-
ing of the larva. The imaginal head, however, with all its specializa-
tion, is still of a more generalized type of structure than is the larval
head. Adaptation for catching live prey in the water has involved a
greater degree of modification than adaptation for catching live prey
in the air. Neither type of head can be regarded as primitive, or even
generalized, but the larval head has departed farther from the gen-
eralized structure because of the more specialized feeding mechanism
of the larva. The metamorphosis of the dragonfly's head gives us a
striking example of how a major part of an insect can be structurally
modified in two different ways to serve the needs of the insect in two
different phases of its life.

II. THE FEEDING APPARATUS

The external feeding organs of the dragonfly larva include the usual
insect mouth parts, namely, the mandibles, the maxillae, the labium,
and the hypopharynx, and also the preoral cibarium. Of these parts
the labium is the only one with a distinctive structure, but its struc-
ture is so extraordinary that it sets the dragonfly larva apart from the
rest of the insects. No other insect or any other animal has developed
its under lip into a protractile organ for grasping living prey.

Mandibles.—The mandibles of an *Anax* larva are strongly toothed

jaws lying horizontally in the space between the labrum and the hypo-
pharynx (fig. 3 A, *Md*). Each mandible is articulated dorsally on the
base of the clypeus and ventrally on the lower margin of the cranium
(fig. 2 B, *a*), and is provided with the usual four muscles of the man-
dible of generalized insects (fig. 3 B), which are a cranial abductor,
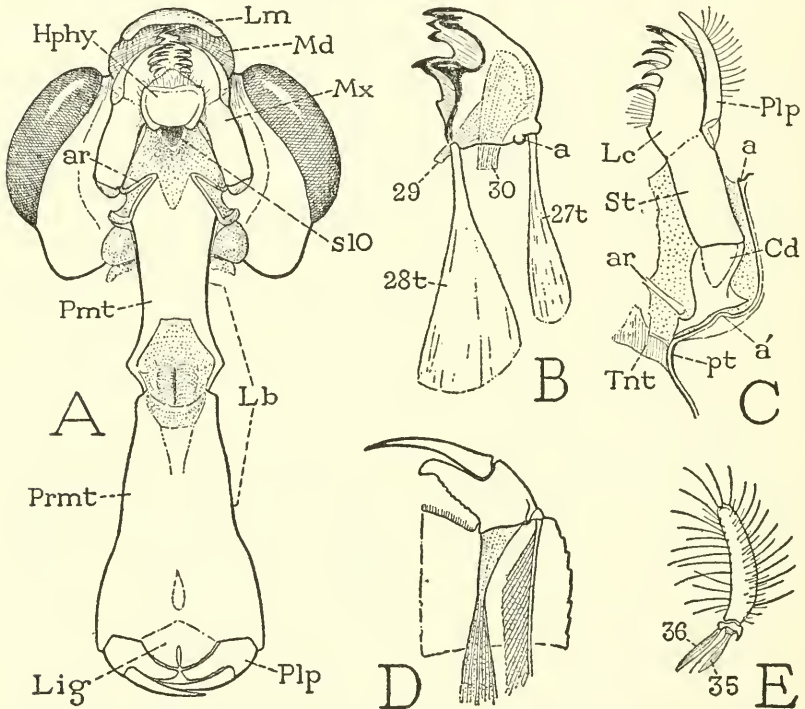

FIG. 3.—*Anax junius* (Drury), larval mouth parts.

A, head, ventral, mouth parts in place, labium extended posteriorly. B, left
mandible, ventral. C, left maxilla, ventral, articulated on margin of cranium.
D, left apical lobe (labial palpus) of prementum. E, maxillary palpus and
muscles of adult.

ar, articular rod of labium; *Cd*, cardo; *Lb*, labium; *Lc*, lacinia; *Lig*, ligula;
Plp, palpus; *Pmt*, postmentum; *Prmt*, prementum; *slO*, opening of salivary
duct; *St*, stipes. Other lettering as on figure 2.

27t, abductor apodeme of mandible; *28t*, adductor apodeme of mandible;
29, hypopharyngeal muscle of mandible; *30*, tentorial muscle of mandible; *35*,
36, muscles of maxillary palpus.

a cranial adductor, a hypopharyngeal muscle, and a tentorial muscle.
The cranial muscles are inserted on broad apodemal tendons (*27t*,
28t), the hypopharyngeal muscle (*29*) arises at the base of the hypo-
pharynx (fig. 4 C) and expands to its attachment on the lateral wall
of the mandible, the tentorial muscle (fig. 3 B, *30*) is attached on the

ventral (posterior) wall of the mandibular cavity. The numerals here used to designate muscles are those given by the writer (1952) to corresponding muscles in the head of the cockroach. The two mandibles of *Anax* are of the same size and shape, have the same dentition, and flat molar areas proximal to the second set of teeth. When the jaws are closed the points of the teeth slightly overlap.

Maxillae.—The larval maxillae are typical generalized maxillary appendages, except for the absence of galeal lobes (fig. 3 C). The sharply toothed laciniae (*Lc*) lie beneath the mandibles (A). A slender outer lobe (C, *Plp*) is sometimes regarded as the galea, but the fact that it is provided with two basal muscles (E) shows that it is the palpus; a galea has but one muscle. The odonate maxillae make the usual maxillary feeding movements of protraction and retraction against the sides of the hypopharynx. In the retracted position (A, *Mx*) the cardines are folded dorsally above the stipites, where they are articulated on the cranial margin (C, *a'*) just in front of the posterior tentorial pits. In protraction the laciniae are thrust forward beyond the mandibles, and they doubtless grasp the prey brought back by the labium to deliver it to the mandibles.

Hypopharynx and cibarium.—The hypopharynx of an *Anax* larva is a relatively small, cushionlike lobe with a flat under surface projecting downward between the anterior ends of the maxillae (fig. 3 A, *Hphy*). It is separated from the base of the labium by a wide membranous space between the maxillary stipites. Just behind its base is a deep pit containing the orifice of the salivary duct (*slO*). The sclerotic lateral walls of the pit are continuous above with the hypopharynx itself, and come together ventrally below the salivary opening to form a V, from which is given off posteriorly a large T-shaped or anchor-shaped apodeme (fig. 4 A, *hAp*). The apodemal support clearly corresponds with the fulcral arc of the hypopharynx of a cockroach, and the apodeme is merely a continuation from it. The common salivary duct (*slDct*) traverses a groove on the dorsal side of the apodeme (D), and on the arms of the apodemal base are inserted the tentorial retractor muscles of the hypopharynx (A, D, *16*). The hypopharyngeal apodeme is a characteristic feature of the dragonfly larva. Its shaft extends posteriorly through the head below the tentorium, and the terminal crossbar is embedded in the posterior lip of the base of the labial postmentum, where it is held in place by small apical brushes of fine fibers. From a process on the under surface of the apodeme arises a pair of long, slender muscles (A, E, *20*) that enter the labium to be inserted on the base of the prementum (fig. 5 A). These muscles evidently correspond with the very short muscles

of the cockroach that go from the hypopharyngeal fulcrum to the prementum. The hypopharyngeal apodeme of the dragonfly larva is clearly a special development functionally correlated with the specialization of the labium; it is either greatly reduced in the adult (fig. 6 G, hAp), or represented by a ligament.
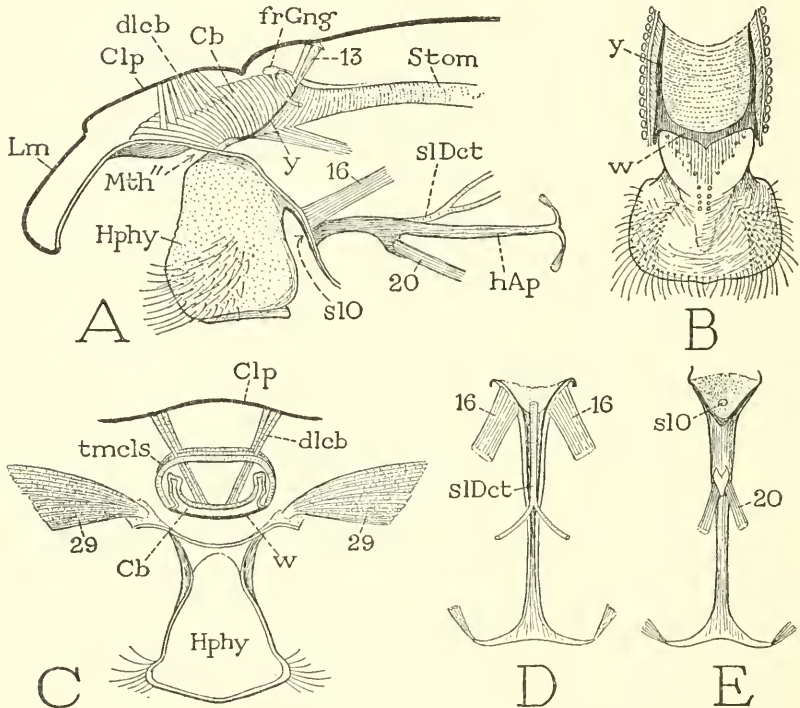

FIG. 4.—*Anax junius* (Drury), hypopharynx and cibarium of larva.

A, longitudinal section of head to left of hypopharynx and cibarium. B, hypopharynx, anterior. C, transverse section through cibarium and hypopharynx, anterior. D, hypopharyngeal apodeme and salivary duct, dorsal. E, hypopharyngeal apodeme, ventral.

Cb, cibarium; *Clp*, clypeus; *dlcb*, dilator muscles of cibarium; *frGng*, frontal ganglion; *hAp*, hypopharyngeal apodeme; *Hphy*, hypopharynx; *Lm*, labrum; *Mth"*, functional mouth; *slDct*, salivary duct; *slO*, opening of salivary duct; *Stom*, stomodaeum; *tmcls*, constrictor muscles of cibarium; *w*, transverse bar of hypopharyngeal suspensorium; *y*, oral arm of same.

13, frontal muscle of hypopharyngeal suspensorium; *16*, tentorial muscle of hypopharyngeal apodeme; *29*, hypopharyngeal muscle of mandible.

The anterior surface of the hypopharynx is continued upward into the floor of a long, preoral cibarial pouch (fig. 4 A, *Cb*), the dorsal wall of which is covered by strong, transverse constrictor muscles. Paired dilator muscles (*dlcb*) arising on the clypeus penetrate between the transverse fibers to be inserted on the cibarial roof (C), which

ordinarily is deeply inflected into the cibarial lumen (*Cb*). The suspensorium of the hypopharynx consists of a transverse bar on the base of the dorsal wall of the hypopharynx (B, *w*), and a pair of lateral arms (*y*) going posteriorly and dorsally along the line of union between the cibarium and the stomodaeum (A) to give attachment to a pair of short frontal muscles (*13*). These suspensorial arms of the hypopharynx mark the site of the true (embryonic) mouth of the insect, which is the opening into the stomodaeum (*Stom*), and lies behind the base of the clypeus (*Clp*). The functional mouth of the dragonfly larva (*Mth"*), opening into the cibarium over the hypopharynx behind the labrum (*Lm*), is therefore a secondary mouth. A full description with illustrations of the cibarial and stomodaeal musculature of the larva of *Ischnura verticalis* is given by Grieve (1937). Since his study was made entirely from microtome sections, this author did not observe the importance of the suspensory arms of the hypopharynx as landmarks for separating the cibarial pouch from the stomodaeum, but he noted that the cibarial muscles are separated from the stomodaeal (pharyngeal) muscles by the frontal ganglion (A, *frGng*) and its brain connectives.

Labium.—The larval labium (fig. 3 A, *Lb*) consists of two major parts hinged on each other by an elbowlike joint. The two parts are the prementum and postmentum of other insects, commonly called "mentum" and "submentum" by writers on odonate anatomy, except Corbet (1953). In most insects the postmentum is a mere plate on the posterior or under side of the head; in the dragonfly larva it is produced into a hollow stalk supporting the prementum, and the whole labium swings back and forth on the base of the postmentum. In an aeschnid larva the labium hangs below the center of the head (fig. 5 C) ; in the retracted position (fig. 1) the elbow lies against the ventral surface of the mesothorax and the prementum is pressed against the under side of the head, from which position it can be thrust out far beyond the head by a forward swing of the postmentum.

The large, spatulate prementum of an *Anax* larva (fig. 3 A, *Prmt*) bears a pair of lateral apical lobes (*Plp*), each armed with a long, sharp hook. These lobes with their hooks are the grasping organs of the larva, but they represent the palpi of an ordinary insect labium since each is provided with an abductor and an adductor muscle (fig. 5 A, *46, 47*). Between their bases is a partially divided median ligular lobe (fig. 3 A, *Lig*). The palpal lobes vary much in size and shape in different genera ; in some anisopterous larvae they are large flaps that form a mask covering the whole face when applied against the head ; in an agrionid they may be slender and elongate and the ligula split

to the middle of the prementum. The abductor muscles of the palpi (fig. 5 A, 46) lie entirely within the prementum as in other insects, but the large adductors (47) break with all the rules of labial anatomy by taking their origins in the distal end of the postmentum. In so doing the adductors acquire an increased power for closing the palpal hooks in the body of the prey, but they disrupt our generalizations on the labial musculature.

The postmentum is supported in the membranous ventral wall of the head behind the maxillae (fig. 3 A, Pmt). Anteriorly its base is produced into a pair of triangular lobes strengthened by lateral marginal thickenings which are extended laterally in the head membrane as a pair of articular rods (ar) that reach to the maxillary cardines (C, Cd), but are not attached to the latter. The true hinge points of the labium on the head are thus at the mesal ends of these rods where the rods join the basal lobes of the postmentum (figs. 3 A, 5 B, h).

The labial musculature of an aeschnid larva has been described, for the most part correctly, by several writers, including Amans (1881), Butler (1904), Whedon (1927), and Munscheid (1933). Four muscles from the head traverse the postmentum to be attached on the base of the prementum (fig. 5 A). The first pair (20) are the long slender muscles arising on the hypopharyngeal apodeme (D). They are inserted on the prementum anterior to the elbow hinge (A, F, 20) and serve as flexors of the prementum on the postmentum. The somewhat thicker muscles of the second pair (A, E, 44) arise on the tentorium (Tnt) and are inserted on leverlike arms (F, lvr) of the premental base that project beyond the elbow hinge; these muscles, therefore, are effective extensors of the prementum. The tentorial muscles are readily identified with the posterior tentorial muscles of the prementum in other insects; the usual accompanying anterior pair are absent in the odonate larva. The apodemal muscles, as already noted, appear to be represented in the cockroach and other orthopteroid insects by the pair of short muscles going from the hypopharyngeal fulcrum below the salivary orifice to the base of the prementum. There are, therefore, in the odonate larva no special muscles developed for the unusual movements of the labium on the head.

A special group of muscles not represented in other insects is present in the elbow region of the larval labium, there being two of these muscles on each side (fig. 5 G). The first (k) is a relatively large, flat muscle arising on the lateral wall of the enlarged distal part of the postmentum, the fibers of which converge to their insertions on the lateral margin of the base of the prementum. This muscle is clearly a secondary flexor of the prementum, as it is termed by
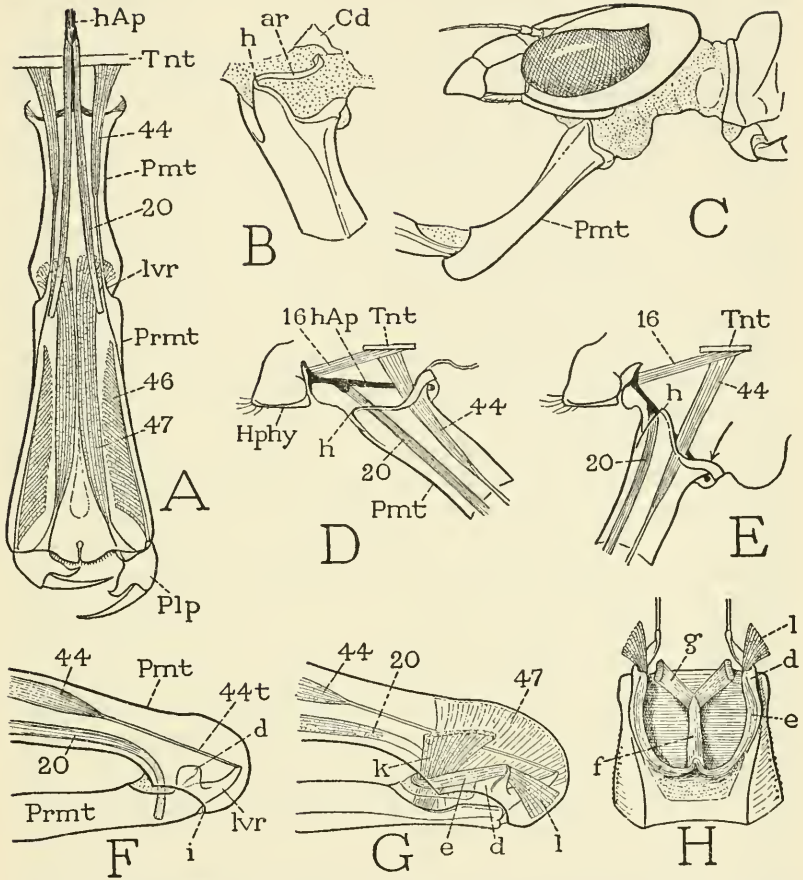
FIG. 5.—*Anax junius* (Drury), larva, structure and mechanism of the labium.

A, the labial musculature, except muscles of the elbow (G). B, base of postmentum, and articular rod, left side. C, head with labium projected. D, diagram of retracted position of postmentum and labial muscles from head. E, same parts in protracted position of postmentum. F, elbow region of labium showing attachment of head muscles on prementum. G, same, showing elbow muscles. H, base of prementum, anterior.

ar, articular rod of labium; *Cd,* cardo; *d,* lobe of lever arm of prementum; *e,* fold of articular membrane; *f,* median tongue of *e; g,* fibrous ligament; *h,* hinge of labium on articular rod; *hAp,* hypopharyngeal apodeme; *Hphy,* hypopharynx; *k,* accessory flexor muscle of prementum; *l,* tensor muscle; *lvr,* lever arm of prementum; *Plp,* palpus; *Pmt,* postmentum; *Prmt,* prementum; *Tnt,* tentorium.

16, tentorial muscle of hypopharyngeal apodeme; *20,* apodemal (flexor) muscle of prementum; *44,* tentorial (extensor) muscle of prementum; *46,* abductor muscle of labial palpus; *47,* adductor muscle of same.

Whedon (1927) and by Munscheid (1933) ; when the prementum is fully extended it is greatly stretched, as shown by these authors. The other elbow muscle is a small, fan-shaped group of fibers (l) arising in the end of the postmentum laterad of the lever arm of the prementum and inserted on the edge of a dorsal lobe (F, G, H, d) of the lever. From the lobe on which this muscle is attached a strongly plicated fold (G, H, e) of the inflected articular membrane of the elbow extends around the anterior side of the joint to the corresponding lever lobe of the opposite side (H). From the middle of the fold a tubular membranous tongue (f) extends proximally between the ends of the great adductor muscles of the palpi, and gives attachment to a pair of thick, divergent, fibrous ligaments (g) attached on two small apodemal knobs of the basal margin of the prementum close to the lever arms. By this structure the palpal adductors are girdled and strongly held in place where they curve upward from the prementum to their origins in the postmentum (G, 47). The muscles (l) attached on the lever lobes (d) are the "secondary extensors" of Whedon, the "tertiary flexors" of Munscheid, but their function would appear to be that of maintaining a tension on the folds (e) that girdle the palpal adductors. The elbow muscles of the odonate larval labium are not comparable to the usual median retractors of the prementum since they lie laterad of the other muscles.

The movements of the labium on the head have generally been attributed to the same muscles that flex and extend the prementum, since no other labial muscles from the head are present. Amans (1881) regarded the muscles from the hypopharyngeal apodeme (fig. 5 D, 20) as the *propulseurs* of the postmentum. Munscheid (1933), on the other hand, attributed the protraction of the labium to the tentorial muscles (44). However, since both pairs of these muscles run posterior to the hinge (h) of the postmentum on the head, it is not clear how either of them could swing the labium forward. Munscheid assumed erroneously that the *Drehpunkt* of the labium lies behind the labial base. Either of the two pairs of labial muscles in contraction might be supposed to effect the retraction of the labium. When the postmentum swings forward (E) it is to be noted that the hypopharyngeal apodeme turns downward, since its crossbar is firmly held in the posterior lip of the postmentum. A downward pressure on the end of the apodeme (arrow in the figure), therefore, turns the postmentum forward on its anterior hinge points (h), and would cause the protraction of the labium if accompanied by an extension of the prementum by the tentorial muscles (44).

It was long ago suggested by Amans (1881) that blood pressure

engendered by a muscular diaphragm in the anterior part of the abdomen effects the opening of the labial hooks. For some reason Amans did not observe the presence of abductor muscles of the palpi. However, it is quite possible, and now seems probable, that his theory of hydraulic action by blood pressure may account for the forward thrust of the entire labium. The abdominal diaphragm that Amans described in the larva of *Aeschna grandis* has been shown by other writers to be present in other anisopterous species. The diaphragm of the *Anax* larva (fig. 9 B, *Dph*) is a strongly developed sheet of transverse muscle fibers closely surrounding the posterior end of the mesenteron (*Ment*) and the ventral tracheal trunks (*vTra*) in the fifth abdominal segment just before the Malpighian tubules. Its ventral margin is stretched between the lower anterior angles of the fifth tergum; the lateral margins extend anteriorly and dorsally along the sides of the fourth segment just below the oblique lateral muscles; the free dorsal edge allows the passage of the dorsal tracheal trunks (*dTra*) and the dorsal blood vessel above it. The diaphragm thus divides the abdominal cavity (fig. 7) into an anterior compartment continuous with the thoracic and head cavities, and a posterior compartment containing the respiratory chamber of the intestine (*rspC*). Since the diaphragm is concave anteriorly, a contraction of its muscles should compress the anterior abdominal chamber. Stretched between the lower anterior angles of the sixth abdominal tergum is a strong transverse muscle (fig. 9 B, *tmcl*) that goes beneath the ileal sac of the intestine behind the Malpighian tubules.

A live *Anax* larva persistently refuses to give any response other than a very slight movement of the labium to pressure on the anterior part of the abdomen or on the thorax. An anesthetized specimen, however, while still limp, reacts at once to compression of the abdomen and thorax by a lifelike forward swing of the postmentum and an extension of the prementum, but neither the palpi nor their hooks are affected by this treatment. The protraction of the labium is accompanied by a strong inflation of the neck membrane at the base of the postmentum (fig. 5 C). It seems evident, therefore, that the protraction of the labium results from blood pressure engendered in the fore part of the body. Munscheid (1933) observes that, when the labium is suddenly protracted, a *Ruck* (quick contraction?) always goes through the body. Perhaps the diaphragm is not the only, or even the chief, source of the pressure, since compression of the thorax has a stronger action on the labium than compression of the abdomen, but the diaphragm at least counteracts the backward extension of the pressure, however the latter may be generated. According to Whedon

(1918) there is no trace of a diaphragm in a zygopterous larva. In these larvae the labium is relatively smaller than in an anisopterous larva, and possibly the narrowness of the abdomen compensates for the absence of a diaphragm.

Evolution of the feeding mechanism.—It is reasonable to suppose that the first step in the evolution of the larval feeding organs consisted of an elongation of the prementum and the conversion of the palpi into grasping organs. The palpi were already provided with abductor and adductor muscles, but to increase the grasping power of the palpi the adductor muscles were greatly enlarged, and, instead of remaining confined to the prementum as in other insects, their bases have transgressed the premento-postmental hinge line and transposed their origins to the distal part of the postmentum. A next step must have been the elongation of the postmentum to form a movable stalk, giving the prementum a greater reach in its new role. The ordinary insect postmentum, however, is immovable, since no head muscles are attached on it. Hence, some accessory mechanism had to be developed in order that the labium could swing on the base of the postmentum. The postmentum acquired articular points with the head on the anterior lip of its base, and to hold it in place, whatever position the labium took, a long, strong apodeme was developed from the base of the hypopharynx with a terminal crossbar imbedded in the posterior lip of the postmental base. Still the postmentum had no motor apparatus. Finally, then, evolution provided a hydraulic mechanism by which blood pressure could be applied against the soft neck membrane behind the base of the postmentum and cause the latter to swing forward on its anterior hinge points with the head. Perhaps in the first place blood pressure was engendered by contraction of the anterior abdominal muscles and the thoracic muscles, but to insure greater efficiency the anterior part of the abdominal cavity was shut off by a strong, transverse muscular diaphragm. Thus at last the complete mechanism of the modern anisopterous larval labium was perfected.

Along with the development of the labial mechanism, the head necessarily underwent an adaptive modification. From a primitive hypognathous condition, preserved in the adult, the larval head became flattened and prognathous so that the prey captured and brought back to the head by the labium could be readily grasped by the protracted maxillae and delivered to the mandibles. The antennae took a more practical position for the larva by being brought forward close to the clypeus.

The question now confronts us as to how we are to visualize the evolution of a complex mechanism such as that of the feeding ap-

paratus of the anisopterous larva, which involves a modification of the head, modifications of the labium such as have occurred in no other insect, the development of a hypopharyngeal apodeme supporting the labium, and the elaboration of a hydraulic mechanism with a muscular diaphragm in the abdomen. Evolution by natural selection is relatively easy to imagine when it pertains to a single organ that might take on a new structure by the gradual addition of small modifications guided to a functional end by the elimination of unfit variations. The matter is quite different, however, when several primarily unrelated parts must all be modified in a correlated manner to work together as a functional unit. The question is further complicated by the necessary condition that a complex of parts can become operative as a whole only when each of the elements is perfected and all are simultaneously adapted to their subsidiary roles.

Metamorphosis of the labium.—At an early stage in the larval transformation the forming imaginal labium begins to retract within the cuticle of the larval labium. At first the imaginal labium has essentially the larval structure (fig. 6 A, *iLb*), but as it continues to retreat and to decrease in size it takes on more of the adult form, until finally it occupies only the narrow basal half of the larval postmentum, where it is compactly rolled upon itself (B, *iLb*). When removed at this stage (C) and spread out (D) the imaginal labium is seen to have completed most of its development, so that little further change is needed to give it the definitive structure (E).

In the transforming labium there takes place, along with the external changes in shape, a reconstruction of the musculature. Munscheid (1933) gives a detailed account of the histolysis and histogenesis of the labial muscles in *Aeschna cyanea,* and a description of the formation of tonofibrillae by which retained muscles are newly attached on the imaginal cuticle. Degeneration of the larval muscles, she says, begins with the dissolution of the myoplasm, but a small part of it, together with a few muscle nuclei, remain as myoblasts for the imaginal muscles, the formation of which takes place relatively early and is quickly completed. Munscheid observes that the transformation of the dragonfly labium gives an example of holometabolism affecting one organ in an insect that is otherwise hemimetabolous, but she evidently did not consider the extreme degree of metamorphosis that takes place also in the skeleton and musculature of the abdomen.

In the transformation of the labium of *Aeschna cyanea,* Munscheid says that two pairs of larval muscles are lost and not replaced in the imago. These muscles are the abductors of the palpi and the tentorial extensors of the prementum. Whedon (1927) says that in *Anax*
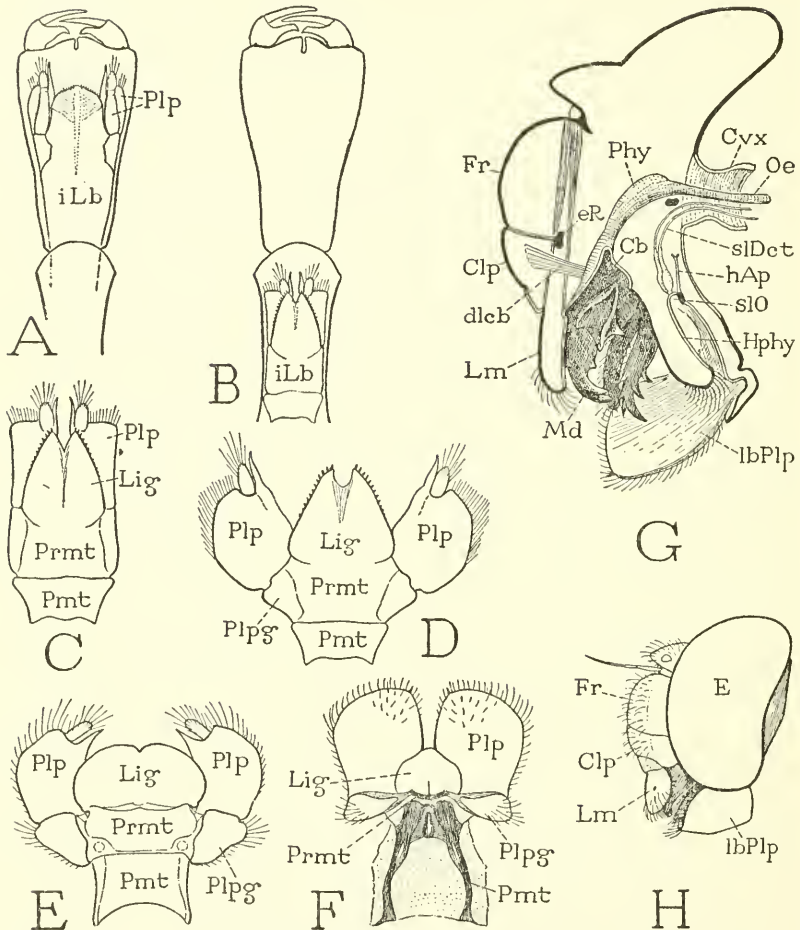
Fig. 6.—Transformation of the labium.

A, labium of a mature *Anax* larva containing the imaginal labium in early stage of transformation. B, same at later stage, imaginal labium retracted into larval postmentum. C, imaginal labium removed from B. D, same unrolled and spread out. E, fully mature imaginal labium. F, imaginal labium of a libellulid. G, section of adult libellulid head. H, head of same, lateral.

Cb, cibarium; *Clp,* clypeus; *Cvx,* neck; *dlcb,* dilator muscle of cibarium; *eR,* epistomal ridge; *Fr,* frons; *iLb,* imaginal labium; *lbPlp,* labial palpus; *Lig,* ligula; *Lm,* labrum; *Md,* mandible; *Oe,* oesophagus; *Phy,* pharynx; *Plp,* palpus; *Plpg,* palpiger; *Pmt,* postmentum; *Prmt,* prementum; *slDct,* salivary duct; *slO,* salivary orifice.

junius the "primary extensors" (tentorial muscles) are retained in the adult, but the pair of muscles he identifies as such are probably the apodemal muscles ("primary flexors"), since he says they arise from a semicircular sclerite near the base of the labium. The apodemal muscles (*20*), because of the shortening or suppression of the apodeme in the adult, as Munscheid shows, come to arise in the imago on the base of the hypopharynx beneath the salivary orifice, which is their normal position in the cockroach. The elbow muscles of the larval labium appear to be retained in the adult.

The labium of the adult dragonfly (fig. 6 E, F), though it has a more generalized structure than that of the larva, is nevertheless specialized in its own way for the purposes of the adult. In particular the large, flat, lobelike palpi, together with the ligula, are evidently adapted for closing in the other mouth parts (G, H) to prevent the escape of captured prey from the mandibles and maxillae.

III. THE ALIMENTARY CANAL

From the mouth at the inner end of the cibarial chamber in the larval head (fig. 7, *Cb*) the slender oesophagus (*Oe*) extends through the head and the thorax, enlarging posteriorly to form a crop (*Cr*), which opens by a narrow neck into the proventriculus (*Prvent*) lying in the first abdominal segment. From the proventriculus the simple, cylindrical ventriculus (*Vent*) goes back to the fifth segment after penetrating the diaphragm (*Dph*), and tapers to its connection with the ileum (*Ilm*). At the junction arise the numerous, threadlike Malpighian tubules (*Mal,* not fully shown in the figure). The ileum turns upward in the fifth segment, close in front of the transverse muscle (*tmcl*) of the abdomen, and expands into an oval sac. The intestine then continues as the huge respiratory chamber (*rspC*), which arises by a narrow extremity from the upper end of the ileal sac and reaches to the end of the eighth abdominal segment. The entrance into the respiratory chamber from the ileum is guarded by three high, convergent folds of the ileal wall. The respiratory chamber is commonly regarded as an enlarged anterior part of the rectum, but the narrow, cylindrical following part of the intestine (*Rect*) has in itself the typical features of the rectum of other insects. The walls of this end chamber alone contain the six characteristic longitudinal thickenings known as rectal pads, and on the intervals between them are attached six rows of dilator muscle fibers arising on the body wall. It is true that the pads are continuous with the six double rows of gills in the respiratory chamber, but there is no reason for regarding the gills as rectal pads. It seems probable, therefore, that the respiratory

chamber should be referred to the colon, and that the end chamber is the true rectum. The anus opens between three small circumanal lobes at the bases of the caudal prongs (fig. 11 G).

At the final metamorphosis of the larva there takes place a total reconstruction of the alimentary canal, details of which have been described by Straub (1943). In the stomodaeum and proctodaeum, after the shedding of the larval intima, reconstruction takes place apparently as in the external parts of the ectoderm by renewed and differentiated growth of the epithelium. In the mesenteron, on the other hand, the larval epithelium itself is cast off and the imaginal epithelium is formed anew from basal regeneration cells, as in most holometabolous insects. At the larval moults, however, Straub finds no evidence of a renewal of the mesenteron epithelium.
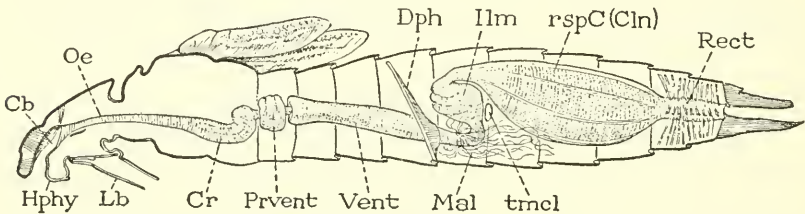

FIG. 7.—*Anax junius* (Drury), the larval alimentary canal.

Cb, cibarium; *Cln*, colon; *Cr*, crop; *Dph*, transverse muscular diaphragm; *Hphy*, hypopharynx; *Ilm*, ileum; *Lb*, labium; *Mal*, Malpighian tubules (not fully shown); *Oe*, oesophagus; *Prvent*, proventriculus; *Rect*, rectum; *rspC*, respiratory chamber; *tmcl*, transverse muscle; *Vent*, ventriculus.

IV. THE THORAX

The thorax of the dragonfly larva is characterized by three special features (fig. 8 A). First is the obliquity of the mesothoracic and metathoracic pleura as indicated by the posterior slant of the pleural sulci from the leg bases to the wings. Second is the almost complete union of the adjoining pleural plates of the wing-bearing segments, resulting in the suppression of an intersegmental groove between the epimeron of the mesothorax and the episternum of the metathorax. Third is the dorsal extension of the upper plates of the mesothoracic episterna (Eps_2) until they meet along the midline of the back in front of the wings, and the corresponding downward extension of the metathoracic epimera (Epm_3) on the ventral surface behind the legs. These features of the thorax evidently have no particular functional significance for the larva, since the larva uses its legs in the ordinary manner for locomotion, and its wings are entirely passive rudiments of the future organs of flight. On the other hand, the thoracic struc-

ture is clearly a functional adaptation for the benefit of the adult ; it must have been early impressed upon the larva, and retained by the larva because it had no disadvantage for the larval activities. By the method of puncture-scarring the larval cuticle, it has been shown by Sargent (1937) that the dorsal extension of the mesepisterna takes
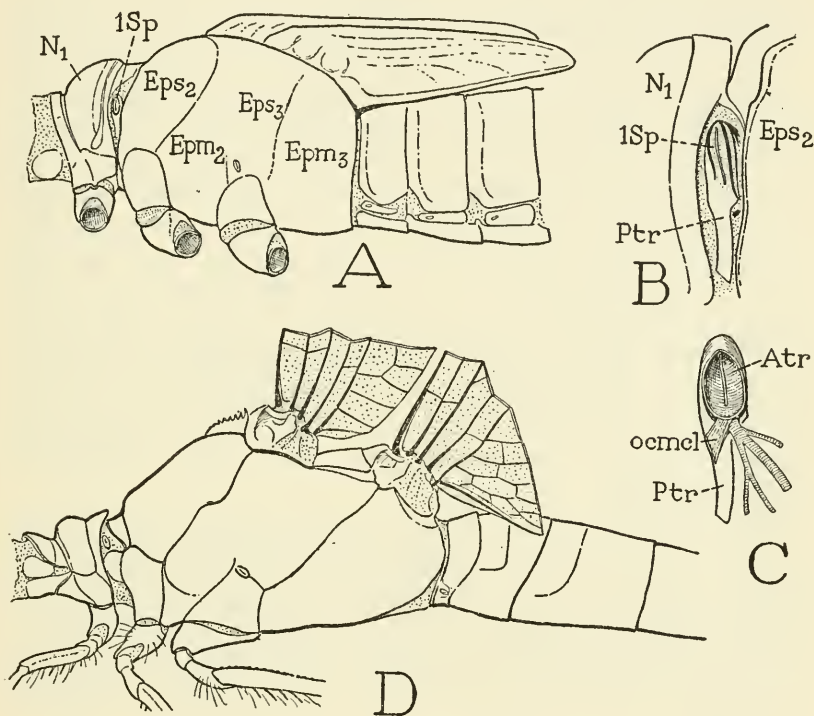

FIG. 8.—The thorax.

A, thorax and base of abdomen of an *Anax* larva. B, first thoracic spiracle of larva, left side, external. C, same spiracle of right side, inner view, main tracheal trunk removed. D, thorax and base of abdomen of an adult libellulid.

Atr, atrium; Epm_2, epimeron of mesothorax, Epm_3, epimeron of metathorax; Eps_2, upper plate of episternum of mesothorax; Eps_2, episternum of metathorax; N_1, pronotum; *ocmcl*, occlusor muscle of spiracle; *Ptr*, peritreme; $1Sp$, first spiracle.

place by marginal growth, while the metepimera increase both by general expansion and by growth of the ventral margins. The post-coxal plate of the metasternum, however, moves bodily backward from the legs as the epipermal plates intervene.

In the adult dragonfly (fig. 8 D) the backward slant of the wing-bearing segments is still more pronounced than in the larva, and a reason for it is now evident. It brings the legs forward in a group

to facilitate their use as organs for entrapping flying prey on the wing, and the wings come to have a posterior position on the back of the thorax, where the weight of the head and thorax is balanced against that of the long, slender abdomen. The union of the two segments converts the pterothorax into a strong framework for the support of the large muscles of flight. The distortion of the thorax is compensated by the extension of the mesothoracic episterna on the back in front of the wings, and that of the metathoracic epimera upon the venter behind the legs. The obliquity of the wing-bearing segments gives to the wing muscles also a strong posterior slant, in contrast to the more usual forward slant of these muscles in other insects. It is well known that the wing mechanism of the Odonata differs from that of other insects in that the muscles that produce the up-and-down movements of the wings are inserted in such manner that they pull directly on the wing bases on opposite sides of the supporting pleural fulcra. A good account of the odonate wing mechanism, briefly stated, is given by Sargent (1951). It is, therefore, possible, but undemonstrated, that the posterior slant of the wing segments has some favorable relation to the special mechanism of the wings; it at least gives greater length to the wing muscles. As a flying machine, the dragonfly is unsurpassed.

Inasmuch as the essential characters of the adult thorax are already present in the thorax of the larva, and are evidently not of any special use to the larva, it would seem that the larval thorax represents an early developmental stage of the imaginal thorax, and, therefore, by contrast with the head and the abdomen, undergoes merely a progressive change rather than a reconstructive change at the transformation to the adult.

The larva possesses the usual two pairs of thoracic spiracles, but only those of the first pair are functional for respiration. These spiracles (fig. 8 A, $1Sp$) are relatively large and lie in the upper parts of long peritremal plates (B, Ptr) between the pronotum and the mesothoracic episterna. The external orifice of each spiracle is a vertical slit opening into an oval atrium (C, Atr), from which is given off directly a large tracheal trunk (removed in the figure), and, from its lower end, a smaller branching trachea. A short occlusor muscle ($ocmcl$) inserted on the ventral margin of the atrium has its origin on the peritreme below the spiracles. Dragonfly larvae sometimes crawl partly out of the water, or entirely at their transformation, and at such times they must breathe through these open anterior spiracles. The other spiracles of the thorax and the abdomen serve on the newly

moulted larval instars only for the withdrawal of the tracheal linings, but they all become functional in the imago.

The principal internal changes that take place in the thorax pertain to the completion of development in the wing muscles, though there is also an elimination of some of the larval neck and leg muscles. The muscles of the larval thorax have been shown by Maloeuf (1935) to be of two types: large, striated functional muscles, which are mostly the muscles of the legs; and slender, unstriated nonfunctional muscles, which are the prospective wing muscles. The number of muscles remains the same throughout the life of the larva, but the number of fibers in individual muscles increases with the larval growth. The wing muscles, Maloeuf says, "grow greatest in fiber number and diameter during the time of the final transformation." The muscle attachments undergo little change during transformation, though "the skeletal parts on which they are attached may become greatly modified." The elaborate endoskeletal system of the adult thorax is said by Sargent (1937) to be developed entirely at the transformation to the imago. The change in the position of the muscles from larva to imago is correlated with the increased obliquity of the thoracic pleura in the adult.

The growth of the wing muscles during the larval life has been described by Marcus (1920), and more fully by Cremer (1934). In the very young larva the wing muscles are said by Cremer to be a hyaline tissue in which are numerous nuclei, but as yet no cell walls or fibrillae. Individual muscle cells appear later, and in the last stage of larval growth the fibrillae are differentiated from the peripheral sarcoplasm. The growth of the muscle cells and the multiplication of fibrillae ends with the beginning of the imaginal stage.

The thoracic musculature of the adult anisopterous dragonfly has been shown by Clark (1940) to include essentially the same muscles that are present in the thorax of other insects, including direct and indirect wing muscles. The dragonflies, however, which do not flex or extend the wings horizontally, appear to have used the direct wing muscles and the tergosternal muscles more efficiently for the up-and-down motion of the wing, rather than depending on vibrations of the terga produced by the dorsal longitudinal and tergosternal muscles, as do most other insects. The intersegmental dorsal muscles are very small as compared with their great size in most other flying insects, including the Ephemeroptera. In the cockroaches, mantids, and termites also, the dorsal muscles are small or absent, but these insects have not developed from the other muscles a motor mechanism for the wings in any degree comparable to that of the dragonflies. Clark

says of the adult anisopterous thoracic musculature that it is "highly specialized, powerful, efficient, and is greatly simplified, when compared with the larval musculature or the more primitive musculature of an orthopteroid insect."

The Odonata as a group clearly stand apart from all other winged insects; the adults were perfect dragonflies in Carboniferous times, but they must have been in the course of their evolution for a vast length of time before their remains are known in the paleontological record. Early in their flying history the dragonflies probably adopted the simple and logical way of moving the wings by the direct pull of muscles on opposite sides of their bases. The method of moving the wings by rhythmically altering the curvature in the wing-bearing tergum depends on several adjustments and modifications in the thoracic skeleton to make it practicable. Yet this second method is that evolved by most of the other insects, and probably in the first place was the simplest method of flapping primitive paranotal lobes.

The legs of an adult dragonfly have two apparent segments in the trochanteral region, but the trochanter of the larva is a single segment with only a suggestion of a proximal constriction.

V. THE ABDOMEN

The abdomen of a larval dragonfly varies in shape and relative size in the various groups, but in every respect it is always much different from the adult abdomen. In the larva of *Anax junius* (fig. 9 A) the abdomen is about twice the length of the head and thorax together. It is expanded toward the middle and tapers posteriorly to the tips of three horny processes enclosing the anus. There are 10 annular segments; the anal processes perhaps represent an eleventh segment. The tergal plates are strongly arched, the sterna slightly convex in the passive position (F).

The chief mechanical functions of the abdomen of an anisopterous larva are respiration and locomotion, both functions being served by the huge gill-bearing sac of the intestine that occupies most of the posterior compartment of the abdominal cavity (fig. 7, *rspC*). In a live larva the branchial chamber may be seen by transmitted light through the abdominal wall making regular expansions and contractions. Water is drawn into the chamber and expelled by way of the rectum and anus. If the water is slowly released, the larva is merely breathing; when it is suddenly and forcibly expelled, the larva darts rapidly forward by jet propulsion from the anus.

The musculature of the branchial chamber consists of bands of longitudinal fibers in its walls running between the gill rows, and of

numerous fine circular fibers, but the sac has no dilator muscles. The branchial chamber, therefore, can contract but it cannot of itself expand. The narrow terminal rectum (fig. 7, *Rect*), however, is provided with six rows of dilator fibers arising on the body wall, as well as with longitudinal and circular fibers in its own walls. This end section of the intestine, therefore, is capable of active expansion and contraction, and, according to Tonner (1936), functions for "swallowing" water and driving it into the respiratory chamber for respiration (*Schluckatmung*). Since the narrow anterior end of the branchial chamber can be closed by the ileal valve, the water may be discharged by the action of the chamber itself. Again, the water is sometimes held in the chamber and agitated or churned for better aeration of the gills (*Kauatmung* of Tonner). The three small circumanal lobes between the bases of the apical processes of the larva (fig. 11 G) apparently act as an anal valve; in a living larva they may be seen actively opening and closing.

The usual breathing movements of the branchial chamber as seen through the body wall are exactly synchronous with dorsoventral and transverse expansions and contractions of the abdominal wall itself, and these skeletal movements appear to be the cause of the ordinary breathing movements of the chamber. On the other hand, when the water is forcibly ejected from the anus, and the larva suddenly darts forward with its legs laid back against the body, it is to be seen that with each spurt the abdomen contracts lengthwise from behind.

The mechanism of the respiratory and locomotory movements may be readily understood by a study of the abdominal skeleton and musculature. The tergal plates of the abdomen are simple, strongly convex arches with slightly projecting lateral margins (fig. 9 F). The sterna are convex, and on the first nine segments each sternum is divided into three parts (A, I), a broad median plate (*mst*), and two small lateral plates (*lst*), which latter are movably hinged on the edges of the tergum and on the median sternal plate. The lateral plates contain the spiracles on the first eight segments, and some writers, therefore, call these plates "pleurites." The term *pleuron,* however, has no very definite meaning as applied to the abdomen, so we may as well distinguish the two sets of ventral plates as *median sternites* and *laterosternites.* The median sternites are almost of uniform width throughout the length of the abdomen (A), but the laterosternites are very small on the anterior segments (J) and largest on the middle region of the abdomen.

The abdominal musculature is strongly developed in the dragonfly larva, and has been fully described by Whedon (1918). It includes
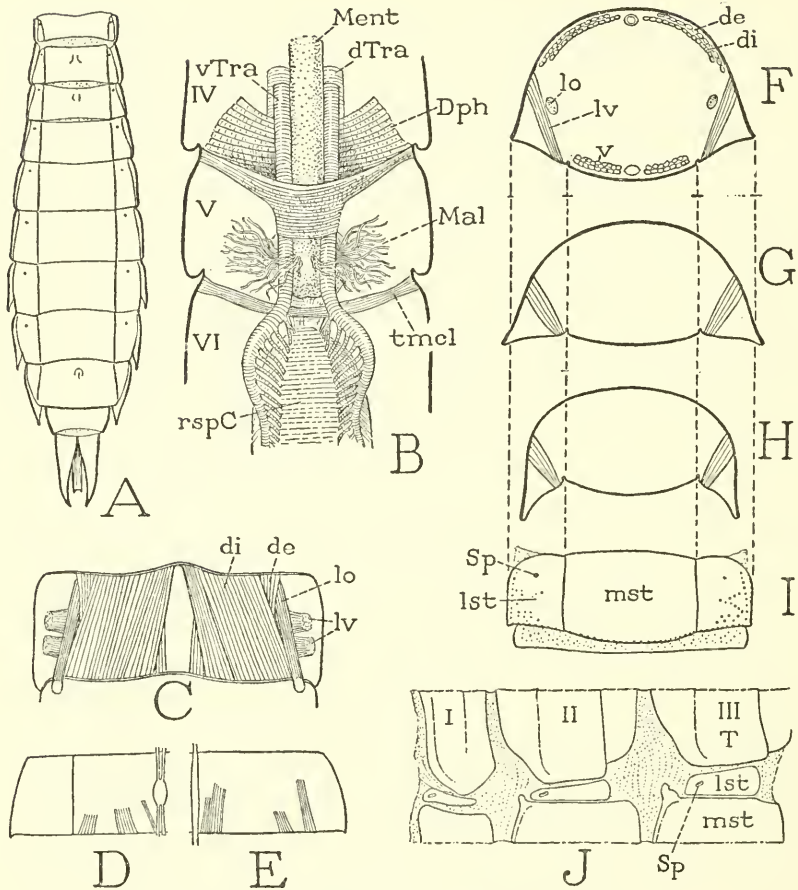
FIG. 9.—The larval abdomen, *Anax junius* (Drury).

A, entire abdomen, ventral. B, segments IV, V, and VI, showing diaphragm and transverse muscle, with associated parts of alimentary canal and tracheal trunks, ventral. C, dorsal and lateral muscles of a typical abdominal segment, ventral. D, E, small outer muscles on sternal and tergal plates of larval abdomen (from Whedon, 1918). F, cross section of a middle segment of abdomen, showing position of muscles. G, same segment contracted as in expiration during mild breathing. H, same segment contracted as in stronger expiration. I, an abdominal sternum, showing its three parts. J, sides of first three abdominal segments.

de, external dorsal muscles; *di*, internal dorsal muscles; *Dph*, diaphragm; *dTra*, dorsal trachea; *lo*, oblique lateral muscle; *lst*, laterosternite; *lv*, vertical lateral muscle; *Mal*, Malpighian tubules (cut off); *Ment*, mesenteron (ventriculus); *mst*, mediosternite; *rspC*, respiratory chamber; *Sp*, spiracle; *tmcl*, transverse muscle; *v*, ventral muscles; *vTra*, ventral trachea.

broad bands of intersegmental dorsal and ventral muscles, and thick tergosternal lateral muscles. The dorsal muscles in each segment are paired layers of external and internal fibers (fig. 9 C, *de, di*) slightly oblique in opposite directions. The ventral muscles are thicker bands of fibers not so definitely arranged in two layers (F, *v*). The lateral muscles include in each segment external, intrasegmental, vertical tergosternal muscles (C, F, *lv*), and a long oblique intersegmental muscle (*lo*) from the side of each tergum in front to the laterosternite of the segment behind. In most of the segments the fibers of the external lateral muscles are grouped on each side in two thick bundles attached on the side of the tergum and inserted on the inner margin of the laterosternite, but in the anterior segments the fibers are less concentrated and some of them attach ventrally on the median sternal plates. Besides these principal abdominal muscles there are also, as shown by Whedon (1918), short outer intersegmental muscles lying close against the tergal and sternal walls (fig. 9 D, E). Finally, in addition to the segmentally repeated muscles, are the muscular diaphragm of the fourth segment (B, *Dph*), the transverse muscle of the sixth segment (*tmcl*), and in the tenth segment special muscles of the apical lobes.

The breathing movements of the larva are most pronounced in the wider posterior half of the abdomen. The expiratory movement includes a slight depression of the tergum accompanied by an expansion of its lower margins, and a much more pronounced retraction of the sternum (fig. 9 G) during which the laterosternites turn upward on the tergal margins. The expiratory muscles, therefore, are the lateral muscles attached on the inner margins of the laterosternites. If the sternum is more strongly retracted (H), the laterosternites turn up at a sharper angle and the tergum is transversely compressed. During inspiration the lateral muscles relax, the tergal arch is restored, the sternum descends and resumes its ventral convexity (F). The action of the muscles is easily seen in a live larva through the semitransparent lateral parts of the abdominal segments.

The inspiratory movements appear to be due in all cases to the elasticity of the tergal plates. Wallengren (1914), however, contended that when the sternum of a segment has reached its maximum inflection, the tergum would be incapable of restoring it to the depressed position. He, therefore, accepted and elaborated the idea of Matula (1911) that the inspiratory movements are caused mostly by contractions of the diaphragm and the transverse muscle. On cutting out a narrow strip of the dorsal integument of the abdomen of a live larva, he observed that, when the insect resumed breathing, the contraction

of these muscles rhythmically brought the cut edges of the back together. From this observation Wallengren concluded that a compression of the terga produced by the diaphragm and the transverse muscle forces the sterna down, and thus causes inspiration. Tonner (1936) likewise claimed that these muscles are the chief effectors of the inspiratory movements, but he contended that the transverse muscle must contract first in order to push down the sterna, after which contraction of the diaphragm can produce only a widening of the posterior segments of the abdomen. Inasmuch as the posterior half of the abdominal cavity is shut off by the diaphragm (fig. 7), a contraction of the transverse muscle (*tmcl*) might be supposed to dilate the segments behind it and thus cause an inflation of the respiratory chamber. However, a breathing larva shows no special movement of the abdomen in the region of the transverse muscle or the diaphragm accompanying inspiration. All the segments uniformly contract and expand, but the respiratory movements are most pronounced in the posterior half of the abdomen.

Artificial respiration practiced on a freshly dead larva shows that no matter how deeply the sternal surface may be pushed in, it automatically bulges out again when the pressure is released. The same movement can be observed in a segmental annulus cleared of the viscera and viewed from one end. If the tergum is held at the top with a fine-pointed forceps, and the sternum is then deeply inflected by artificial pressure, the lateral margins of the tergum are drawn in (fig. 9 H) ; on release of the pressure the sides of the tergum at once spring outward and the sternum goes down to the passive position (F). Observation of a live larva quietly breathing shows that the elevation and depression of the sterna are accompanied by corresponding but smaller movements of the terga and a slight extension and regression of the lateral tergal margins, just as a rubber bulb artificially compressed expands by its own elasticity. The only muscles that effect a respiratory movement, therefore, are the lateral tergosternal muscles that flex the laterosternites on the terga. There is no evidence or reason for believing that the diaphragm and the transverse muscle play any essential part in respiration. Inspiration is due to the elasticity of the arched tergal plates, expiration results from the inflection of the sterna by the lateral tergosternal muscles. The diaphragm and transverse muscle are known to exist only in anisopterous larvae. Since the diaphragm most probably is functionally related to the protraction of the labium, a respiratory function need not be attributed to it in order to give it a reason for being.

The forcible ejection of water from the rectum for purposes of

locomotion may in part result from an intensification of the abdominal expiratory movement of respiration, but the conspicuous abdominal movement seen as the larva darts forward in the water is the lengthwise contraction of the abdominal segments from behind. The principal locomotor force exerted on the inflated respiratory chamber, therefore, evidently results from contraction of the bands of dorsal and ventral intersegmental muscles. These muscles, as already noted, are strongly developed in the larva, but they are totally lost after the transformation to the adult, showing that they are of functional importance only in the larval stage. It is possible, however, that the transverse muscle and perhaps the diaphragm assist in the expulsive contraction of the abdomen.

Inasmuch as the modern anisopterous and zygopterous larvae are mainly differentiated by their manner of breathing, the question naturally arises as to how the primary odonate larva accomplished respiration when it first took to the water. The fact that the labial mechanism is the same in both groups of larva and is a device for catching aquatic prey shows that the larvae were differeniated in their modern respiratory methods after the labium was perfected as a grasping organ. Yet, some means of breathing in the water must have been the first adaptation necessary for an insect on its adoption of an aquatic life. The answer to the question may possibly be furnished by those modern zygopterous larvae that have tracheated gill appendages along the sides of the abdomen, such as the species of *Cora* (fig. 11 D) described by Calvert (1911), or *Euphaea variagata* described by Ris (1912), who concludes these appendages are clearly respiratory organs since each is filled with a rich tracheal arborization. Calvert says, "We have good grounds for looking on *Cora* and its allies as being in many respects the most primitive of living Odonata." It is not impossible or even improbable, therefore, that the primary odonate larva developed tracheal gills along the sides of the abdomen, and that in this respect it resembled the larvae of modern mayflies. We can further imagine that these gills of the early larvae of both the Ephemeroptera and the Odonata were primarily abdominal styli inherited from terrestrial ancestors, such as those still preserved on the terrestrial Thysanura.

The caudal appendages of young zygopterous larvae are slender processes, which, according to Tillyard (1917), become triquetral in the second or third instar, and in subsequent instars are flattened to form the lamellar gills (fig. 11 A). In some forms, however, the appendages remain as slender, horny processes (B) that certainly can have no respiratory function. In those larvae mentioned above hav-

ing lateral abdominal gills (D) the caudal appendages are large vesiculate lobes. Ris (1912) describes them as ovoid vesicles with thin outer walls, and an internal alveolar structure penetrated by blood canals and tracheae, but he draws no conclusion as to their function. Tillyard says the saccoid gills are formed by inflation of the triquetral form. It is said that even the appendages that are evidently gills in function may be broken off without any apparent effect on the activity of the mutilated individual. It would seem, therefore, that the caudal appendages of the zygopterous larva may have been first developed perhaps as locomotor organs and were later modified in most species for respiratory purposes.

Zygopterous larvae are said by Tillyard (1917) to have a supplementary rectal respiration, which is particularly vigorous in a newly hatched larva, and which in larvae that have lost their caudal gills "can be watched by a careful use of carmine particles." By "respiration" evidently is meant an inhalation and exhalation of water through the anus. The walls of the rectum, Tillyard says, are thrown into three longitudinal folds of high columnar cells, but the folds are not tracheated and can serve only as blood gills. It may be supposed, then, that intestinal respiration was first tried out as a substitute for external branchial respiration, and was later perfected in the anisopterous group by the development of tracheated folds within a prerectal sac, while in the others the caudal appendages were modified for respiration, though in a few forms the primitive lateral gills were retained. Since use of the respiratory sac for locomotion is a specialty of anisopterous larvae, and depends on abdominal contraction, it probably followed as a secondary function of the sac.

At the transformation of the larva to the adult, both the skeleton and the musculature of the abdomen undergo a complete reorganization. The simple arched segmental tergum of the larva (fig. 9 F) becomes much flattened in the adult (fig. 10 A) with a ridge along the dorsal midline, and the lateral parts sharply folded onto the ventral surface in two sections, first horizontally, and then dorsally to form the lateral walls of a deep median channel containing the sternum (S). The broad, three-part larval sternum is replaced in the imago by a narrow median plate (B, S), widened anteriorly where it bears on each side two lateral apodemal processes, and tapered posteriorly to an apical point. The laterosternites of the larva have entirely disappeared as such, and the spiracles of the adult (Sp) are contained in membranous conjunctivae between the sterna and the inflected tergal margins.

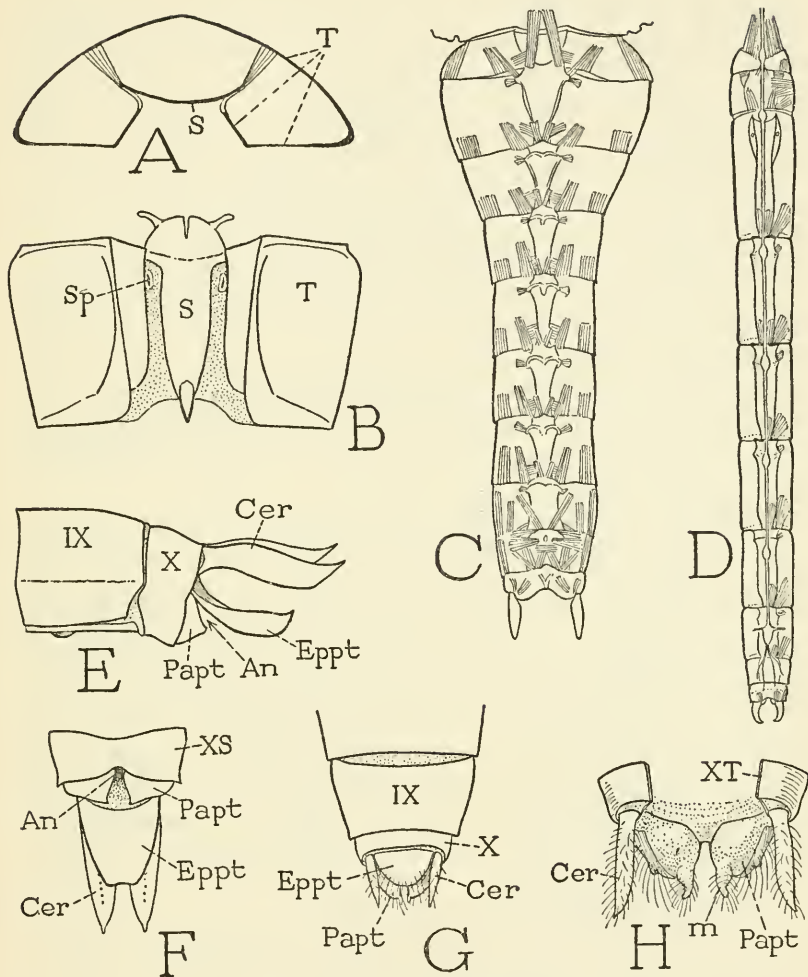The strong dorsal, ventral, and lateral musculature of the larval

FIG. 10.—The adult abdomen.

A, cross section of abdominal segment of a libellulid. B, ventral view of same. C, ventral musculature of abdomen of female *Anax junius* (from Whedon, 1918). D, ventral musculature shown on right side of abdomen of *Calopteryx maculata* (from Whedon, 1918). E, end segments and terminal appendages of male libellulid. F, ventral view of same. G, terminal structure of abdomen of female libellulid. H, apical lobes of same, ventral.

An, anus; *Cer,* cercus ("cercoid"); *Eppt,* epiproct; *m,* process of paraproct; *Papt,* paraproct; *S,* sternum; *Sp,* spiracle; *T,* tergum.

abdomen is wholly destroyed with the transformation to the imago, though, according to Whedon (1929), the dissolution is not completed until some time after ecdysis of the adult, about three days in *Anax junius.* The adult musculature of the abdomen, as shown by Plateau (1884) in *Agrion,* and as more fully described by Whedon (1918), in both Zygoptera and Anisoptera (fig. 10 C, D), is surprisingly simple considering the various uses the adults make of the abdomen in mating and egg laying. The intersegmental muscles are short, well-separated groups of fibers arising on the posterior part of the segment in front and inserting on the anterior margin of the segment behind. These muscles, Whedon (1929) says, are derived from the small outermost muscles of the larval abdomen. The sterna of the adult are provided with small anterior and posterior muscles arising on the terga, which probably are expiratory in function. Only in the posterior genital segments in both sexes and the anterior genital segment of the male is there a more elaborate musculature, perhaps representing newly formed muscles of the imago.

The musculature of the dragonfly larval abdomen is of particular interest in that it consists of two distinct sets of muscles, those of one set being highly developed for purposes of the larva and destroyed in the imago, those of the other set being carried over into the adult to become the principal intersegmental muscles of the imaginal abdomen. It would appear that there is thus no transformation of purely larval muscles into imaginal muscles. Still more curious is the fact that the principal musculature of the larval abdomen has the structure of the usual intersegmental musculature of the abdomen in other insects. The abdominal musculature, therefore, must be at an early stage of development differentiated into larval muscles and prospective imaginal muscles.

The striking difference between the skeletal structure of the odonate larval abdomen and that of the adult abdomen suggests that the pattern of sclerotization in the insect integument is merely an adaptation to mechanical function. Nevertheless, it would be of interest to know what parts of the odonate larval abdominal integument become specific parts of the imaginal integument, if this could be determined at the transformation by the method of scarring the larval integument, as has been done in the case of the eyes and the thorax.

Considering the extent of the skeletal and muscle changes that takes place at the transformation from larva to adult in both the head and the abdomen, the development of the wing muscles in the thorax, and the reconstruction of the alimentary canal and tracheal system, the total reorganization of the dragonfly during its transforming period

amounts to a remarkable degree of metamorphosis in an insect commonly said to be "hemimetabolous."

The terminal structures of the larval abdomen and their adult equiv-
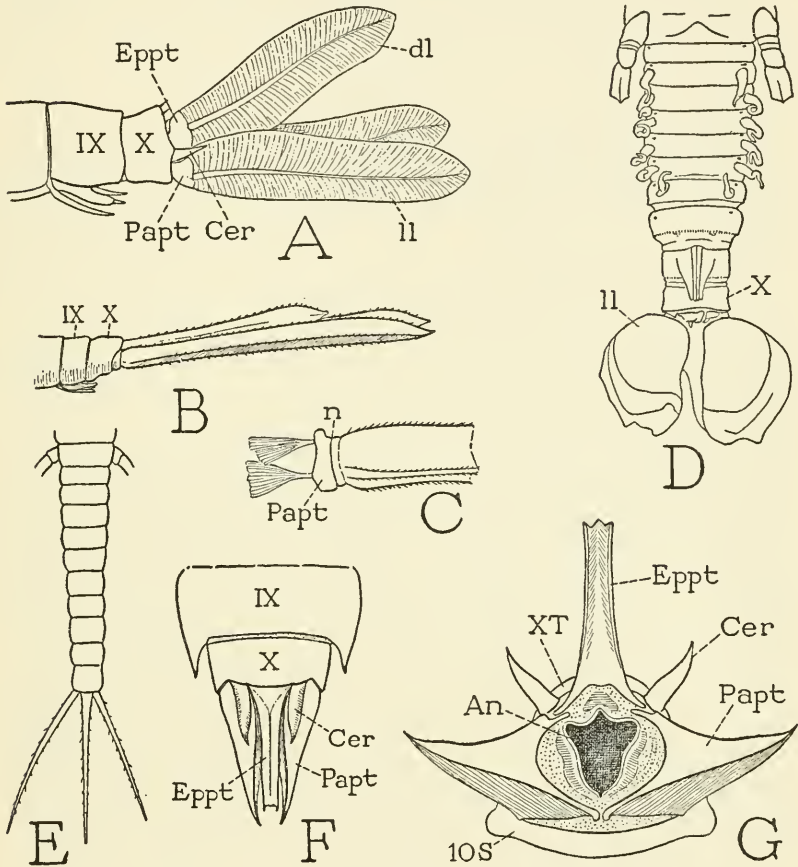

FIG. 11.—Terminal structures of odonate larvae.

A, *Archilestes grandis* (Rambur), end segments and gills. B, *Agrion virgo* L., end segments and apical lobes. C, same, base of apical lobe. D, *Cora* sp., abdomen of larva with vesicular apical lobes, ventral (from Calvert, 1911). E, abdomen of young larva of *Calopteryx* sp., dorsal (from Heymons, 1904). F, *Anax junius* (Drury), end segments and apical lobes. G, same, end of abdomen with apical lobes spread apart, showing three small circumanal valves.

An, anus; *Cer,* cercus ("cercoid"); *dl,* dorsal gill lobe; *Eppt,* epiproct; *ll,* lateral gill lobe; *n,* base of apical lobe of *Agrion virgo;* *Papt,* paraproct; *S,* sternum. *T,* tergum.

alents are of interest because of the different interpretations of their homologies that have been given to them. The three tapering horny lobes that enclose the anus of the anisopterous larva (fig. 11 F) appear superficially to correspond with the epiproct and paraprocts of

other insects. Dorsally at the sides of the median lobe is a pair of smaller appendages (*Cer*) that have the exact relative position of the usual abdominal cerci. However, most students of Odonata, following Heymons (1904), regard the lateral anal lobes as the true cerci and the dorsal cercuslike appendages as secondary structures, which are termed "cercoids." The reason for this interpretation as given by Heymons is that the "cercoids" are not present in early larval stages, and that the lateral anal lobes in some young zygopterous larvae (E) are long filaments resembling the filamentous cerci of Thysanura and larvae of mayflies and stoneflies. Neither of these facts, however, is necessarily evidence that the "cercoids" are not the cerci of odonate larvae.

At the transformation of the male anisopterous larva to the adult, the "cercoids" become the superior claspers (fig. 10 E, F, *Cer*), the dorsal anal lobe (*Eppt*) becomes the so-called "inferior" clasper, which arises above the anus (*An*), and the lateral anal lobes of the larva become small triangular plates lying at the sides of the anus (*Papt*). It seems incredible that these lateral plates of the adult can be cerci; they have the exact position of paraprocts relative to the "inferior" clasper and the anus, and there can be no question that the "inferior" clasper is the epiproct. Schmidt (1933) accepts Heymon's interpretation that the dorsal appendages are "cercoids," but he regards the paraproctial plates of the adult as sternal plates of the eleventh segment, which they probably are, and he contends that the "true cerci" are small processes arising from the membranous inner surfaces of these plates (fig. 10 H, *m*). These processes of the paraprocts are shown by Asahina (1949) to be of unusual size, though but little sclerotized, in both the male and the female of the anisozygopteron *Epiophlebia superstes*. Since true cerci in other insects never have any such relation to the sternum as these paraproctial processes have to the paraprocts, this last interpretation is hardly acceptable. On anatomical evidence, therefore, the writer sees no reason for not regarding the "cercoids" as true cerci, and the anal lobes as the epiproct and the paraprocts in both the larva and the adult. This interpretation of the terminal structures of Anisoptera has been maintained also by Crampton (1918) and by Handlirsch (1926). In an adult anisopterous female the end of the abdomen (fig. 10 G) is so typically orthopteroid that it might pass for that of a grasshopper or a cricket.

The apical appendages of zygopterous larvae, whether of the broad lamellar form (fig. 11 A) or of the slender triquetral type (B), are supported on basal plates (A, *Eppt, Papt*) that evidently are the true epiproct and paraprocts. Each appendage is separated from its sup-

porting plate by a distinct circular groove (C, *n*) and is readily broken off at the base. The median appendage (A, *dl*) must be admitted to be a secondary outgrowth of the epiproct; the presence of similar appendages (*ll*) on the lateral basal plates is then no evidence that the latter are not paraprocts likewise bearing secondary outgrowths.

SUMMARY

1. The larval and the adult dragonfly have evolved independently along divergent lines, the larva in adaptation to life in the water, the adult to life in the air, until the two have become so different that they might pass for unrelated animals. The egg, however, retains the dual potentiality of redeveloping both the larva and the adult, each one in its latest evolutionary stage.

2. The larval adaptation has affected the head, the labium, the alimentary canal, the tracheal system, the muscular system, and the abdomen.

3. In correlation with the mechanism of protraction and retraction of the highly modified larval labium, there has been developed from the base of the hypopharynx a large T-shaped apodeme with its crossbar imbedded in the posterior lip of the base of the postmentum. This apodeme controls the movements of the larval labium; it is greatly reduced in the adult or replaced by a ligament.

4. In protraction and retraction the labium swings on anterior points of its base in the ventral head membrane. Neither of the two pairs of labial muscles from the head can produce the movement of protraction, since they enter the postmentum *behind* the axis on which the labium swings, but either pair or both pairs may cause retraction of the labium. It is suggested, therefore, that the abdominal diaphragm between the fourth and fifth segments of the abdomen plays an important part in the mechanism of labial protraction. Compression of the anterior part of the abdomen and the rear part of the thorax of a freshly anesthetized larva at once protracts the labium and inflates the neck behind the labium. If blood pressure extends the labium of a live larva in this manner, the diaphragm at least prevents the backward expenditure of the pressure, and probably contributes something to the forward pressure.

5. No evidence was observed that the diaphragm has any respiratory function in the aeschnid larva. Expansion and contraction of the abdomen appear to be due entirely to the lateral tergosternal muscles and the elasticity of the arched tergal plates of the abdominal segments.

6. The respiratory chamber of the intestine is probably the colon rather than the rectum, the latter forming only the terminal region of the intestine connecting the respiratory chamber with the anus.

7. The "cercoids" are here regarded as true cerci, and the anal lobes as epiproct and paraprocts. The caudal gills of zygopterous larvae are lobes of the epiproct and paraprocts. The primitive respiratory organs of odonate larvae were probably paired lateral gills of the abdomen, which are still retained in some modern species.

8. Only the thorax of the larva resembles the corresponding part of the adult; the larval head and abdomen are constructed entirely for purposes of the aquatic larva, the thorax serves equally well for both larva and adult.

9. The similarity of the thoracic structure in both larva and adult suggests that the primitive young dragonfly, before it took to the water, resembled the adult as much as any modern terrestrial nymph resembles its parents, but probably at that time the adults had not yet attained the status of perfect dragonflies.

10. The metamorphic changes of the aeschnid larva in its transformation to the imago are equivalent in degree to those of many holometabolous insects. The head, the labium, and the abdomen are entirely made over, the alimentary canal and the tracheal system are simplified, the labial muscles are histolysed and re-formed, the great mass of larval muscles in the abdomen are destroyed and not replaced in the adult, the thoracic wing muscles simply complete their development, the reproductive organs mature.

11. The transformation that produces the imago within the cuticle of the last larval instar is entirely comparable in degree to that which takes place in the pupa of a so-called holometabolous insect; though it is completed without a subsequent moult, the transforming stage is equivalent to a pupa, and is a preliminary stage of the adult.

12. The dragonfly larva should be an interesting subject for experimental studies on the role played by hormones in metamorphosis.

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